PARAPHYLY AND ENDEMIC GENERA OF OCEANIC ISLANDS: IMPLICATIONS FOR CONSERVATION[1]

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ABSTRACT

Genera of flowering plants that are endemic to oceanic islands are often of great biological interest. These groups represent adaptive complexes that confer distinction to the islands or archipelagos in which they are found, and this often results in a focus on their conservation. In recent decades, numerous molecular phylogenetic (and other evolutionary) studies have been done on island genera, hence providing much valuable new information on relationships and evolution of island groups. Genera restricted to oceanic islands derive evolutionarily from parental stocks usually in continental regions. These parental genera are often themselves evolutionarily successful, being particularly adept at dispersal, adaptation, and speciation. These immigrants to isolated oceanic islands derive from common ancestors of large and diverse parents or directly from within the lineages themselves. If in the latter case the island derivatives are treated at the generic level, then the parental genus becomes paraphyletic in a cladistic sense. In this circumstance there are three alternatives to classification of the island group: (1) treat both the island complex as a distinct holophyletic genus and the progenitor as a coordinate, but paraphyletic, genus; (2) submerge the island complex into the parental genus, perhaps at the subgeneric or sectional level, creating a larger holophyletic genus; or (3) divide the parental genus and island complex into a series of smaller genera in such a manner that all become holophyletic. A synthesis of recent investigations on 100 endemic island genera and relatives was completed in the Bonin Islands, Canary Islands, Galápagos Islands, Hawaiian Islands, Madeiran Islands, Robinson Crusoe Islands, and St. Helena. The results show that 64 genera are still accepted and remain uninvestigated or are seen as holophyletic in phylogenetic analyses. Seven have already been submerged based on non-cladistic results, and 29 are viewed as being nested within larger parental genera. Of this latter group, 15 of the genera are still being recognized at this time; six have been recommended as belonging within their parental genera; and eight have been formally transferred into the progenitor genera with combinations made. If further actions were to be taken based on strict holophyly, following the second alternative mentioned above, then these 29 genera would disappear as endemics in their islands or archipelagos. This would result in an overall average drop of 31.9% endemic genera in oceanic islands worldwide (based on the sample analyzed). With the third alternative, new generic concepts for the island and progenitor taxa would need to be worked out. Instead of recognizing genera on the basis of simple holophyly, genera should be based on cohesiveness, distinctness, and monophyly s.l. (i.e., including paraphyly and holophyly). A statistic is provided as a means for making these assessments quantitatively. The importance of unique and/or divergent character change for classification of island lineages is also stressed.

Key words: Adaptations, cohesiveness, distinctness, generic limits, holophyly, island evolution, monophyly, paraphyly, predictive quality.

Oceanic islands are fascinating natural laboratories for the study of evolution and biogeography. Surrounded by water, these volcanic land masses offer opportunities for understanding dispersal, divergence, adaptive radiation, and speciation. Over millions of years in isolation from continental relatives, island populations diverge to such an extent morphologically that they are considered taxonomically distinct species. With even more geological time and more morphological divergence, endemic genera result. One of the attractions of island floras, in fact, has been the high levels of endemic species and genera that they contain. Most studies of processes of evolution in archipelagos

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focus on endemic taxa, because these are the systems that have evolved in situ. Furthermore, conservation priorities in oceanic islands often focus on investigating and preserving populations of these endemic taxa. They are, in effect, regarded as the biological treasures of these island ecosystems due to their morphological uniqueness.

New molecular phylogenetic (and other evolutionary) studies have now provided much new information on relationships among island taxa and their continental relatives. This has led to more insights on evolutionary relationships of endemic taxa. In a phylogenetic context, this has provided more precise assessment of holophyly and paraphyly (Hörandl & Stuessy, 2010) than was ever before possible. This applies not only to the island endemics, but also to the continental relatives, or progenitors.

Considerable discussion has prevailed over the merits of holophyly and paraphyly in biological classification. Many workers admit only holophyletic groups in classification on the grounds that this is the only way to have classification related precisely to phylogeny, and vice versa (Hennig, 1966; Ebach & Williams, 2004; Schmidt-Lebuhn, 2011; Wiley & Lieberman, 2011). Strict adherence to a branching topology as an evolutionary explanation does provide a clear basis for hierarchical classification, but it does not take evolutionary divergence within lineages into account. Workers who believe that this evolutionary information should also be incorporated into biological classification may elect to recognize both holophyletic and paraphyletic groups (Stuessy, 1997; Brummitt, 2002; Hörandl, 2007; Hörandl & Stuessy, 2010).

Application of strict holophyly is of particular importance at the generic level. Many studies over the past several decades, especially in view of new molecular data and phylogenetic analyses, have led to generic remodeling. If a genus is shown to be paraphyletic, the solutions have been either to lump together the units involved into one larger genus, or to split up the group into several (or even many) smaller holophyletic genera. In oceanic islands, the latter approach could lead to an increase in numbers of island endemic genera. The former approach, however, would see the submergence of formerly endemic island genera into larger continental genera.

Evidence to date suggests that there is a tendency for lumping island endemic genera into larger continental relatives. The island genera are derived by dispersal and divergence from continental progenitors. Because of the speed of the divergence, it might be that the island genera are genetically not so divergent from the continental relatives, but they are usually very divergent morphologically, hence their recognition at the generic level. As an example, in the Robinson Crusoe (Juan Fernández) Islands, recently the two largest endemic genera, *Robinsonia* and *Dendroseris* (Compositae) with seven and 11 endemic species, respectively, were transferred into the large *Senecio* (Pelser et al., 2007, 2010a, 2010b) and *Sonchus* (Mejías & Kim, 2012) genera.

It is appropriate, therefore, to examine the impact that application of concepts of holophyly, based primarily on molecular phylogenetic analyses, has already had, or might potentially have, on levels of generic endemism in oceanic archipelagos worldwide. Depending upon how broad the effects might be, these actions could have a substantial impact on world island conservation. Furthermore, as genetic endemism is a criterion for delimitation of floristic zones (e.g., Takhtajan, 1986), a reduction in endemic genera in oceanic islands might also have an impact on the classification of world vegetation.

Therefore, the objectives of this paper are to: (1) inventory the genera endemic to representative archipelagos of the world, viz., Bonin Islands (Japan), Canary Islands (Spain), Galápagos Islands (Ecuador), Hawaiian Islands (U.S.A.), Madeiran Islands (Portugal), Robinson Crusoe Islands (Chile), and St. Helena (United Kingdom); (2) survey the endemic genera in these archipelagos that have new molecular phylogenetic (or other recent evolutionary) studies; (3) determine the effect that adherence to strict holophyly will (or might) have on existing generic limits and, therefore, on potential conservation mandates; and (4) suggest a method other than strict holophyly for evaluation of generic limits as determined by predictive quality (defined by a combination of monophyly s.l., distinctness, and cohesiveness).

Genera Endemic to Oceanic Archipelagos

The first step in examining the status of endemic genera in oceanic islands of the world is to obtain an inventory of the taxa. We concentrate on angiosperms only, as these have similar patterns of biogeography and evolutionary divergence that contrast with these aspects in the ferns (e.g., Stuessy et al., 1990).

We have elected to examine seven different oceanic island systems that are representative of size, complexity, and geographical position, and that also have had at least some recent molecular phylogenetic attention. These are (with political affinities): Bonin Islands (Japan), Canary Islands (Spain), Galápagos Islands (Ecuador), Hawaiian Islands (U.S.A.), Madeiran Islands (Portugal), Robinson Crusoe (= Juan Fernández) Islands (Chile), and St. Helena (United Kingdom). Lists of endemic genera were developed by consulting major floristic

Table 1. Total number of endemic angiosperm genera and included species of selected oceanic islands or archipelagos.

Island/Archipelago	Number of endemic genera	Number of included species
Hawaiian Islands	34	344
Canary Islands	30	150
Robinson Crusoe Islands	12	31
St. Helena	10	15
Galápagos Islands	7	25
Madeiran Islands	5	9
Bonin Islands	2	3
Totals	**100**	**577**

treatments for these islands/archipelagos as follows: Bonin Islands (Ono & Kobayashi, 1985), Canary Islands (Hansen & Sunding, 1993), Galápagos Islands (Wiggins & Porter, 1971), Hawaiian Islands (Wagner et al., 1999), Madeiran Islands (Press & Short, 1994), Robinson Crusoe Islands (Marticorena et al., 1998; Danton et al., 2006), and St. Helena (Cronk, 2000).

A summary of genera endemic in these selected oceanic islands is given in Table 1. A total of 100 genera has been described and recognized in these seven islands/archipelagos. The Hawaiian Islands contain the most (34) genera and the small Bonin Islands the fewest (2). In general, the degree of generic divergence (and endemism) relates to the size of the island chain and its isolation from source areas. The number of included species in these endemic genera is 577, with 59% of these being in the Hawaiian Islands. Levels of specific diversity in islands relate directly to elevation and habitat heterogeneity (Stuessy et al., 2006). This large number of species is also of interest in that should the genera be remodeled due to holophyly (or other reasons), names of some of these endemics would perforce need to be changed, which would create some inconvenience with conservation agendas.

Recent Molecular Phylogenetic (or Other Evolutionary) Studies on Endemic Genera and Their Taxonomic Impact

In this molecular age, it is hardly surprising that a significant number of studies have focused on phylogenetic (and broader evolutionary) relationships within endemic island genera and among these genera and their presumptive continental relatives. Within the genera, the focus has obviously been on resolving affinities among the endemic species, particularly to assess specific monophyly s.l., evaluate character evolution, and infer modes of speciation. Among genera, the objective has been principally to determine biogeographic connections and resolve taxonomic issues at the generic level. This section of the paper examines these new investigations (summarized in Table 2) and reveals their implications for the taxonomic status of endemic genera in selected oceanic islands and archipelagos.

Bonin Islands

These islands, also known as the Osagawara Islands, are an archipelago of 20 small land masses located approximately 1000 km south of mainland Japan. They harbor a total flora of 460 taxa of vascular plants, of which 30% are endemic (Ono, 1998), including two endemic genera, *Dendrocacalia* and *Boninia* (Ito, 1998). *Dendrocacalia* (Compositae, Senecioneae), a dioecious tree consisting of only one species, *D. crepidifolia*, is restricted to Haha Island within the archipelago (Kato & Nagamasu, 1996). A recent molecular phylogenetic survey of tribe Senecioneae (Pelser et al., 2007) included *Dendrocacalia*, and it resolved sister to *Arrhenechthites novoguineensis*. However, due to conflicts between nuclear and plastic gene markers, as well as the consideration of the existence of many smaller genera in relation to the huge *Senecio*, much more study is needed before generic limits in this tribe can be finalized. In the meantime, *Dendrocacalia* remains independent and, hence, as an endemic genus in the Bonin Islands. It is treated as distinct in the recent Compositae book (Funk et al., 2009).

The other endemic genus described for the Bonin Islands has been *Boninia* (Rutaceae), described originally by Planchon (1872), and consisting of two species, *B. grisea* and *B. glabra*. Morphological studies on these species, which were treated within a recent revision of the related genera *Euodia* and *Melicope* (Hartley, 2001), have revealed that *B. glabra* is actually a taxonomic synonym of *M. quadrilocularis*. *Boninia grisea* remains as a good species, but based on morphology, it appears to fall more properly within the large *Melicope* as *M. grisea*. Harbaugh et al. (2009) have examined molecular phylogenetic relationships within *Melicope*, but no samples of the former *Boninia* were included. Evidence to date, therefore, suggests that *Boninia* should be included within *Melicope*, and the former disappears as an endemic genus in the Bonin Islands.

Canary Islands

The Canary Islands, belonging to Spain, and being a favorite holiday destination for Europeans, have received considerable molecular phylogenetic (and other evolutionary) attention. There are 30 endemic

Table 2. Genera of angiosperms considered previously to be endemic to representative oceanic islands/archipelagos of the world and recent molecular phylogenetic (or other evolutionary) studies.

Island group and endemic genus	Family	Number of species	References
Bonin Islands			
Boninia	Rutaceae	2	Hartley, 2001
Dendrocacalia	Compositae, Senecioneae	1	Pelser et al., 2007
Canary Islands			
Aeonium	Crassulaceae	38 (plus 1 in Africa and 1 in Madeira)	Mes et al., 1997; Mort et al., 2001, 2002
Aichryson	Crassulaceae	10	Mes et al., 1997; Mort et al., 2001, 2002
Allagopappus	Compositae, Inuleae	2	Andrus et al., 2004
Argyranthemum	Compositae, Anthemideae	24	Francisco-Ortega et al., 1995a, 1995b, 1997
Atalanthus (= *Taeckholmia*)	Compositae, Lactuceae	8	Whitton et al., 1995; Kim et al., 1996a, 1996b, 2007
Babcockia	Compositae, Lactuceae	1	Whitton et al., 1995; Kim et al., 1996a, 1996b, 2007
Benconia	Rosaceae	4	Helfgott et al., 2000
Bethencourtia	Compositae, Senecioneae	2	Pelser et al., 2007, 2010
Bystropogon	Lamiaceae	7	Trusty et al., 2004, 2005
Dendriopoterium	Rosaceae	2	Helfgott et al., 2000
Dicheranthus	Caryophyllaceae	1	Fior et al., 2006
Gesnouinia	Urticaceae	1	Monro, 2006; Hadiah et al., 2008
Gonospermum	Compositae, Anthemideae	4	Francisco-Ortega et al., 2001a
Greenovia	Crassulaceae	4	Mes et al., 1997; Mort et al. 2001, 2002; Kim et al., 2008
Heywoodiella	Compositae, Lactuceae	1	Lack, 1978
Ixanthus	Gentianaceae	1	Thiv et al., 1999
Kunkeliella	Santalaceae	4	Der & Nickrent, 2008
Lactucosonchus	Compositae, Lactuceae	1	Whitton et al., 1995; Kim et al., 1996a, 1996b, 2007
Lugoa	Compositae, Anthemideae	1	Francisco-Ortega et al., 2001a
Marcetella	Rosaceae	2	Helfgott et al., 2000
Monanthes	Crassulaceae	18	Mes et al., 1997; Mort et al., 2001, 2002
Neochamaelea	Rutaceae	1	Appelhans et al., 2010
Parolinia	Brassicaceae	2	—
Plocama	Rubiaceae	1	Backlund et al., 2007
Schizogyne	Compositae, Inuleae	2	Francisco-Ortega et al., 2001b
Spartocytisus	Leguminosae	2	Cubas et al., 2002; Pardo et al., 2004
Sventenia	Compositae, Lactuceae	1	Whitton et al., 1995; Kim et al., 1996a, 1996b, 2007
Tinguarra	Umbelliferae	2	Downie et al., 2000; Spalik et al., 2001
Todaroa	Umbelliferae	1	Downie et al., 2000; Spalik et al., 2001
Vieraea	Compositae, Inuleae	1	Francisco-Ortega et al., 2001b; Andrus et al., 2004
Galápagos Islands			
Brachycereus	Cactaceae	1	Lendel et al., 2006
Darwiniothamnus	Compositae, Astereae	3	Andrus et al., 2009
Jasminocereus	Cactaceae	1	Applequist & Wallace, 2002; Lendel et al., 2006
Lecocarpus	Compositae, Millerieae	3	Blöch et al., 2009; Stuessy et al., 2011
Scalesia	Compositae, Heliantheae	15	Schilling et al., 1994
Sicyocaulis	Curcurbitaceae	1	Sebastian et al., 2010
Trigonopterum	Compositae, Ecliptinae	1	Panero et al., 1999; Wagner & Robinson, 2001
Hawaiian Islands			
Alsinodendron	Caryophyllaceae	4	Wagner et al., 2005
Argyroxiphium	Compositae, Madieae	5	Baldwin, 2003
Bobea	Rubiaceae, Guettardeae	4	Achille et al., 2006; Bremer & Eriksson, 2009
Brighamia	Campanulaceae	2	Givnish et al., 1995, 2009; Antonelli, 2008
Broussaisia	Hydrangeaceae	1	Hufford et al., 2001; Xiang et al., 2011

Table 2. Continued.

Island group and endemic genus	Family	Number of species	References
Clermontia	Campanulaceae	22	Givnish et al., 1995, 2009; Antonelli, 2008
Cyanea	Campanulaceae	52	Givnish et al., 1995, 2009; Antonelli, 2008
Delissea	Campanulaceae	9	Givnish et al., 1995, 2009; Antonelli, 2008
Dissochondrus	Gramineae	1	—
Dubautia	Compositae, Madieae	21	Baldwin, 2003
Haplostachys	Labiatae	5	Lindqvist & Albert, 2002; Lindqvist et al., 2003; Scheen et al., 2010
Hesperomannia	Compositae, Vernonieae	3	Kim et al., 1998; Keeley et al., 2007
Hibiscadelphus	Malvaceae	7	—
Hillebrandia	Begoniaceae	1	Clement et al., 2004; Forrest et al., 2005
Isodendrion	Violaceae	4	Tokuoka, 2008
Kokia	Malvaceae	4	Seelanan et al., 1997; Pfeil et al., 2002
Labordia	Loganiaceae	15	Bremer & Struwe, 1992; Motley & Carr, 1998; Backlund et al., 2000
Lipochaeta	Compositae, Heliantheae	6	Rabakonandrianina, 1980; Rabakonandrianina & Carr, 1981; Panero et al., 1999; Wagner & Robinson, 2001
Munroidendron	Araliaceae	1	Plunkett et al., 2001, 2004a, 2004b; Lowry & Plunkett, 2010; Plunkett & Lowry, 2010
Neraudia	Urticaceae	5	—
Nothocestrum	Solanaceae	4	Olmstead et al., 2008
Nototrichium	Amaranthaceae	3	Kadereit et al., 2003; Müller & Borsch, 2005; Ogundipe & Chase, 2009
Pelea	Rutaceae	48 (plus 2 in Marquesas)	Hartley & Stone, 1989; Hartley, 2001
Phyllostegia	Labiatae	32 (plus 1 in Tahiti)	Lindqvist & Albert, 2002; Lindqvist et al., 2003; Scheen et al., 2010
Platydesma	Rutaceae	4	Hartley, 2001; Harbaugh et al., 2009
Pteralyxia	Apocynaceae	2	Livschultz et al., 2007
Remya	Compositae, Astereae	3	Karaman-Castro & Urbatsch, 2009
Rollandia	Campanulaceae	8	Lammers et al., 1993; Givnish et al., 1995
Schiedea	Caryophyllaceae	34	Wagner et al., 1995, 1999, 2005; Soltis et al., 1996; Weller et al., 2001; Kapralov & Filatov, 2006; Sakai et al., 2006; Willyard et al., 2011
Stenogyne	Labiatae	20	Lindqvist & Albert, 2002; Lindqvist et al., 2003; Scheen et al., 2010
Tetraplasandra	Araliaceae	7	Costello & Motley, 2001, 2007
Touchardia	Urticaceae	1	Monro, 2006
Trematolobelia	Campanulaceae	4	Givnish et al., 2009; Lammers, 2009
Wilkesia	Compositae, Madieae	2	Baldwin, 2003
Madeiran Islands			
Chamaemeles	Rosaceae	1	—
Monizia	Umbelliferae	1	Spalik & Downie, 2007
Musschia	Campanulaceae	2	Roquet et al., 2008
Parafestuca	Gramineae	1	Quintanar et al., 2006
Sinapidendron	Cruciferae	4	Warwick & Black, 1993; Warwick & Sauder, 2005
Robinson Crusoe Islands			
Centaurodendron	Compositae, Cardueae	2	Susanna et al., 2011
Cuminia	Labiatae	2	Trusty et al., 2004; Bräuchler et al., 2010
Dendroseris	Compositae, Lactuceae	11	Kim et al., 2007; Mejías & Kim, in press
Juania	Palmae	1	—
Lactoris	Lactoridaceae	1	Soltis et al., 1997, 2011; Gonzalez & Rudall, 2001; Wanke et al., 2006
×*Margyracaena*	Rosaceae	1	Crawford et al., 1993
Megalachne	Gramineae	2	—

Table 2. Continued.

Island group and endemic genus	Family	Number of species	References
Nothomyrcia	Myrtaceae	1	Murilla-Aldana & Ruiz, 2011; Murillo-A. et al., 2012
Rhetinodendron	Compositae, Senecioneae	1	Pacheco et al., 1985; Sanders et al., 1987; Sang et al., 1995; Pelser et al., 2007, 2010b
Robinsonia	Compositae, Senecioneae	7	Pelser et al., 2007, 2010b
Selkirkia	Boraginaceae	1	—
Yunquea	Compositae, Cardueae	1	—
St. Helena			
Commidendrum	Compositae, Astereae	4	Eastwood et al., 2004
Lachanodes	Compositae, Senecioneae	1	Pelser et al., 2010a
Melanodendron	Compositae, Astereae	1	Eastwood et al., 2004
Mellissia	Solanaceae	1	Olmstead et al., 2008
Nesiota	Rhamnaceae	1	—
Nesohedyotis	Rubiaceae	1	Bremer & Eriksson, 2009; Groeninckx et al., 2009
Petrobium	Compositae, Coreopsideae	1	Ryding & Bremer, 1992; Kimball & Crawford, 2004
Pladaroxylon	Compositae, Senecioneae	1	Pelser et al., 2010a
Trimeris	Campanulaceae	1	Lammers, 2011
Trochetiopsis	Sterculiaceae	3	—

genera, including *Aeonium* (Crassulaceae) being mostly endemic (with one species also in Africa). Several genera are more properly endemic to Macaronesia, which includes the Madeiran Islands, Salvage Islands, and also the Azores.

One endemic genus, *Parolinia* (Brassicaceae), with two recognized species, *P. glabriuscula* and *P. platypetala*, has not yet been investigated in a modern phylogenetic context. Patterns of isozymic genetic variation in both species, however, have been examined (Fernandez-Palacios et al., 2004). Morphological studies have allied *Parolinia* variously with *Diceratella*, *Leiospora*, *Maresia*, *Morettia*, etc. (Al-Shehbaz et al., 2006).

Two genera have been removed from the endemic ranks based on non-cladistic (or non-molecular) investigations. *Heywoodiella* (Compositae, Lactuceae) was described by Sventenius and Bramwell (1971) as endemic to the one island, Tenerife, but earlier comparative morphological and cytological investigations (Lack, 1978) have shown it to be a species of *Hypochaeris*, which has ca. 15 species in the Mediterranean region plus 41 in South America (E. Urtubey et al., in prep.). *Neochamaelea* (Rutaceae) is another monospecific genus, in this case related to *Cneorum*. Recent comparative morphological studies (Appelhans et al., 2010) have led to synonymizing *Neochamaelea* into *Cneorum*.

Two endemic species of *Senecio*, *S. hermosae* and *S. palmensis*, were earlier placed in a separate endemic genus, *Bethencourtia* (Compositae, Senecioneae), by Choisy (in Buch, 1825). These were subsequently brought back to *Senecio* but kept as a distinct section by de Candolle (1838). Nordenstam (2006) again elevated the section to generic level, plus adding a new species, but he coined the name *Canariothamnus*, because he believed *Bethencourtia* to be invalidly published (apparently because it was not accepted by Buch in the original work). A closer nomenclatural examination (Nordenstam in Greuter & Raab-Straube, 2006), however, revealed that *Bethencourtia* was, indeed, validly published because it was accepted by the describing author, Choisy (1825), hence relegating the recent *Canariothamnus* to synonymy. Molecular phylogenetic studies (ITS) of *Senecio* (Pelser et al., 2007) have shown *Bethencourtia* to form a small holophyletic group, which ties closest with species of *Jacobaea* (from Eurasia) and then with sub-Saharan African species of *Senecio*. With ITS/ETS combined data (Pelser et al., 2010a), *B. palmensis*, *J. vulgaris*, and *S. lineatus* form a well-supported clade (97% bootstrap support [BS]). With plastid data (Pelser et al., 2010a: 863), *Bethencourtia* is given as "sister to *Emilia*" (77% BS; table 3). Due to the many species of *Senecio* and uncertainty regarding how to properly circumscribe genera in this massive complex, no further taxonomic action has been taken at this point. At the present time, therefore, *Bethencourtia* remains an endemic genus in the Canary Islands.

Many of the recent molecular phylogenetic studies on endemic genera have confirmed holophyly for

several of them; therefore, they retain endemic status. *Gesnouinia* (Urticaceae) is a monospecific genus (*G. arborea*) examined in context of molecular phylogenetic studies on the entire family using *rbcL* and *trnL-F* chloroplast markers (Monro, 2006; Hadiah et al., 2008). The genus appears as one of the basal lineages, tying with good support (100% BS) to *Parietaria pensylvanica*, and these both nested in a polytomy with three other genera (Monro, 2006). *Bystropogon* (Lamiaceae) consists of seven species, with two restricted to the Madeiran Islands. Recent molecular phylogenetic studies with ITS, 5.8S, *trnL*, and *trnL-trnF* (Trusty et al., 2004, 2005) reveal the genus to be holophyletic (with moderate BS). *Dicheranthus* (Caryophyllaceae) is a monospecific (*D. plocamoides*) genus of tribe Paronychieae (Bittrich, 1993). Molecular phylogenetic investigations with *matK* and ITS (Fior et al., 2006) reveal the genus to be sister to *Pteranthus dichotomus*. *Ixanthus* (Gentianaceae) is a monospecific endemic genus of uncertain generic affinities generally within subtribe Gentianinae (Yuan & Küpfer, 1995). Molecular phylogenetic studies by Thiv et al. (1999), using ITS and *matK*, however, show *I. viscosus* to be sister to three species of *Blackstonia* (total four species from Europe and the Mediterranean region), and within subtribes Erythraeinae or Chironiinae.

Three of the endemic holophyletic genera are in Compositae. One of the largest genera in the Canary Islands is *Argyranthemum* (Anthemideae) with 24 species endemic to Macaronesia. Twenty species are endemic to the Canary Islands proper, with four others found in the Madeiran Islands, Salvage Islands, and the Azores. ITS (Francisco-Ortega et al., 1997) and chloroplast DNA (cpDNA) studies (Francisco-Ortega et al., 1995a, 1995b, 1997) have confirmed holophyly of this genus, which ties to a clade that includes species of *Heteranthemis*, *Ismelia*, and *Chrysanthemum*. *Vieraea* is a monospecific (*V. laevigata*) endemic genus belonging to tribe Inuleae and related to *Pulicaria*. Molecular phylogenetic studies using ITS (Francisco-Ortega et al., 2001b; Andrus et al., 2004) have examined these and related genera and show that the genus is sister (74% BS) to *Perralderia coronopifolia*, representing a genus of three species of northwestern Africa (Mabberley, 2008). On morphological grounds, *Vieraea* appears closer to *Pulicaria vieraeoides* (Andrus et al., 2004). *Allagopappus* is a bispecific endemic genus also of tribe Inuleae. In the same study by Andrus et al. (2004) using ITS sequences, *Allagopappus* resolves in a distinct basalmost Macaronesian lineage and, therefore, is still recognized as endemic in the archipelago.

Other genera have been investigated with new methods and represent possible taxonomic changes, but the authors involved have not yet taken formal actions. *Kunkeliella* (Santalaceae) is a genus of four species that is close to *Thesium* and related genera (Stearn, 1972). The new molecular phylogenetic studies (Der & Nickrent, 2008), however, show *K. subsucculenta* to be sister to *Thesidium* (*T. fragile*) and these two sister to two analyzed species of *Thesium* in the "Thesium Clade." *Kunkeliella*, therefore, at this time remains a good endemic genus, although Stearn (1972) suggested that as another alternative, it might be regarded as a new section of *Thesium*.

Within the archipelago is a conspicuous woody Compositae alliance of 11 species centered around *Sonchus* that includes the endemic genera *Babcockia*, *Lactucosonchus*, *Sventenia*, and *Taeckholmia*, the first three being monospecific and the last with eight species. *Taeckholmia* has now been combined into *Atalanthus* (Hansen & Sunding, 1993: 6), because the former name was discovered to be illegitimate. Whitton et al. (1995), using cpDNA restriction site data, began to obtain a clearer view of relationships among genera within the tribe, and Kim et al. (1999) followed with cpDNA (*psbA-trnH* intergenic spacer) sequences that gave somewhat better resolution. ITS data (Kim et al., 1996a, 1996b), however, have provided even more resolution. The four genera in question were accepted as distinct by Bremer (1993, 1994), and they were also listed in Kilian et al. (2009) but with the indication that generic limits relating to *Sonchus* need to be reconsidered. These same authors, however, in an appendix to their work (p. 381), listed all these endemic genera as synonyms under *Sonchus* but without combinations for included species. Kim et al. (2007), using ITS and *matK* sequences, show clearly that *Babcockia*, *Lactucosonchus*, and *Sventenia* fall within *Sonchus*, and that it was their intention to eventually make such transfers, the genera being reduced to subgenera. Such transfers have apparently not yet been completed, however.

The subtribe Gonosperminae of Compositae consists of three genera, two of which are endemic to the Canary Islands: *Gonospermum* (four species) and *Lugoa* (one species). All these species have been examined by ITS markers (Francisco-Ortega et al., 2001a) in comparison to related genera of tribe Anthemideae, and the results show that these two genera form a holophyletic group, although not highly supported. *Lugoa* falls within *Gonospermum*, and the former, therefore, is suggested to be an indistinct genus, but the formal combinations have not yet been

made. *Gonospermum* is holophyletic if *Lugoa* is combined into it.

Crassulaceae have long attracted attention for the many morphologically interesting endemic species in the Canary Islands, as well as in all of Macaronesia. The endemic (or nearly so) genera include *Aeonium* (38 species, plus one from Madeira and another from eastern Africa; Liu, 1989), *Aichryson* (10 species, with three species confined to the Madeiran Islands, and one also occurring in the Azores), *Greenovia* (four species), and *Monanthes* (18 species). That this forms a large holophyletic assemblage has been determined earlier by Mort et al. (2001). The relationships among the genera, however, have now also been examined (Mort et al., 2002) by ITS and several cpDNA regions (*matK*, and *trnL-trnF* and *psbA-trnH* spacers). The results show *Aichryson* to be holophyletic and sister to the other genera. *Monanthes* is nearly holophyletic, with *M. icterica* slightly more basal in the cladogram. This species was earlier shown to be somewhat divergent with ITS as well (Mes et al., 1997). *Aeonium* is solidly in one clade, but it is considered paraphyletic, because *Greenovia* (itself holophyletic) is nested inside and sister to *A. viscatum* and then next allied to *A. saundersii*. Mort et al. (2002) suggest including *Greenovia* into *Aeonium*, but no formal transfers have yet been made. Kim et al. (2008) also refer to *Aeonium* in the sense of *Greenovia* being included within it.

Spartocytisus (Leguminosae) with two species is an endemic genus related to *Cytisus* and allied genera. Molecular phylogenetic studies (Cubas et al., 2002) using ITS and *trnL-trnF* spacer show *S. supranubius* to be sister to a large clade with species of *Cytisus*, but including also a smaller holophyletic *Calicotome* and *Chamaecytisus proliferus*. Outside the clade fall other genera and five other species of *Cytisus*. The authors suggest that *Spartocytisus* might be "better considered as a separate section within *Cytisus* (i.e., sect. *Oreosparton*)" (Cubas et al., 2002: 239). Relationships of *Spartocytisus* were again examined by a study with the same markers but focusing on *Genista* and allied genera (Pardo et al., 2004); no change in relationships for *Spartocytisus* was observed.

Several molecular phylogenetic studies have resulted in new insights and taxonomic changes on relationships for endemic genera in the Canary Islands. *Plocama* (Rubiaceae) is an endemic monospecific genus (*P. pendula*) with morphological affinities with the genera *Crocyllis*, *Kellogia*, *Neogaillonia*, and *Putoria* in "Group 1" of tribe Paederieae (Puff, 1982). Molecular phylogenetic studies (Backlund et al., 2007) on genera of Paederieae using cp *rbcL*, *rps16* intron, and *trnT-F* show *Plocama* to form a small clade with *Crocyllis* and species of *Gaillonia* (*G. yemenensis* and *G. tinctoria*). The authors point to the importance of a larger clade, however, that includes also the genera *Putoria*, *Pterogaillonia*, *Pseudogaillonia*, *Aitchisonia*, *Jaubertia*, and *Choulettia*, the group being accorded tribal recognition as Putorieae. All these genera, however, have now been combined into one genus, as this basal node has high BS support (100%). The authors also stress that diagnostic morphological features to characterize these genera have been difficult to find. As *Plocama* is the earliest generic name, the genus has now been expanded from one to 34 species, and it ceases being a Canarian endemic.

Tinguarra (Umbelliferae) with two endemic species is confined to the Canary Islands (*T. sicula* from Europe was earlier submerged into *Athamanta* [Tutin, 1968], but this has not been entirely accepted [e.g., Knees, 1996]). Downie et al. (2000), using ITS1 and 2 sequences, showed close affinities of *Tinguarra* with *Athamanta*, a genus of about five Mediterranean species (Mabberley, 2008), suggesting that the two might be treated as a single genus (along with *Todaroa*). Combining ITS data with morphological and anatomical characters, Spalik et al. (2001) clearly showed *Tinguarra* to be sister to *Athamanta* and made formal transfers of *T. cerviariaefolia* and *T. montana* into *Athamanta* as section *Tinguarra*. The monospecific *Todaroa* (Umbelliferae) remains isolated in analysis with ITS plus morphological and anatomical data (Spalik et al., 2001), and hence still remains an endemic genus in the archipelago.

Finally, in a few instances the new molecular data and phylogenetic analyses have simply not yet been able to revolve relationships of some of the endemic genera, and more work will obviously be needed in the future. *Bencomia*, *Dendriopoterium*, and *Marcetella* are endemic genera of Rosaceae in Macaronesia, the former two genera including four and two species, respectively, from the Canary Islands. *Marcetella* has one species endemic to the Canary Islands (*M. moquiniana*) and one to Madeira and the Azores (*M. maderensis*). Molecular phylogenetic studies (Helfgott et al., 2000) based on ITS show this *Bencomia* alliance to be holophyletic and well supported (100% BS). *Dendriopoterium* and *Marcetella* were at one time (Nordberg, 1966) placed as sections together within *Sanguisorba* as subgenus *Dendriopoterium*, but *Bencomia* was left as a distinct genus. The ITS data poorly resolve the *Bencomia* alliance and, therefore, at this time these genera remain endemic to the islands. The data do show, however, that none of the genera belong in *Sanguisorba*.

Schizogyne (Compositae, Inuleae), with two species, is endemic to the Canary Islands (*S. sericea* being also known in the Salvage Islands; Hansen & Sunding, 1993), along with *Allagopappus* and *Vieraea*. Molecular phylogenetic studies using ITS (Francisco-Ortega et al., 2001b) reveal that *Schizogyne* is sister to three species of *Pulicaria*, which itself appears to be biphyletic, and together with the monospecific *Limbarda crithmoides* from Europe all form a good clade. No taxonomic actions have yet been implemented from these results, however, and *Schizogyne*, therefore, remains an endemic genus at this time.

Galápagos Islands

These well-known islands contain 309 genera of angiosperms (Wiggins & Porter, 1971), of which only seven are regarded as endemic (Table 1). In general, there have been few molecular phylogenetic investigations in the Galápagos Islands, perhaps due to restrictions on collecting activities in the archipelago. At present, all of the recognized endemic genera remain undisturbed with regard to taxonomic status. This includes genera documented as sister groups to other genera, as well as those nested within larger continental genera.

There are two endemic genera of cacti, *Brachycereus* and *Jasminocereus*, each with only one species (but the latter with three recognized varieties). These two genera apparently are closely related to each other and have affinities to *Armatocereus* from coastal Ecuador and Peru (Anderson, 2001, from a statement based on DNA sequences communicated by R. Wallace). Barthlott and Hunt (1993), however, placed *Jasminocereus* in tribe Browningeae and *Brachycereus* in Trochocereae. Some molecular sequence studies have been published dealing with Cactaceae (e.g., Nyffeler, 2002; Arias et al., 2005), but neither endemic genus from the Galápagos was sampled for these investigations. Applequist and Wallace (2002), however, did include *Jasminocereus* using data on deletions in the intergenic spacer *trnT-trnL* chloroplast region, but the tribal placement of this endemic genus is not well indicated. Lendel et al. (2006), in an online abstract, reported that based on cp *trnK* intron (including *matK*) and *rps16* intron, *Brachycereus* and *Jasminocereus* form a strongly supported group sister to *Armatocereus*. For the time being, at least, these two species of cacti remain as endemic genera in the islands.

Scalesia (Compositae, Heliantheae), the largest endemic plant genus in the islands with approximately 15 species, appears to be a monophyletic assemblage based on morphological and cytological data (Eliasson, 1974). Based on cpDNA restriction site analyses (Schilling et al., 1994), *Scalesia* relates to *Pappobolus* on the South American continent. Only one species of *Scalesia*, the abundant *S. pedunculata*, however, was sampled, and the authors admit that the conclusions are somewhat tenuous.

Four genera, *Darwiniothamnus*, *Lecocarpus*, *Sicyocaulis*, and *Trigonopterum*, have been shown from molecular phylogenetic studies to be nested within larger parental genera. Despite these perspectives, however, the genera have not been submerged at this time (with or without formal combinations). *Darwiniothamnus* (Compositae, Astereae) is a shrubby endemic genus of three species. Molecular phylogenetic studies using ITS (Andrus et al., 2009) have demonstrated it to be biphyletic, with *D. lancifolius* and *D. tenuifolius* relating to *Erigeron bellidiastroides* of the Caribbean region, and with *D. alternifolius* tying to two Chilean species of *Erigeron*. The authors do not state that *Darwiniothamnus* should be submerged into *Erigeron*, but as a biphyletic entity deriving from two different clades of this latter genus, there could hardly be any other alternative if holophyly were applied as a classificatory perspective for this group. At the present time, however, *Darwiniothamnus* still survives as an endemic genus in the archipelago.

Lecocarpus, another woody endemic genus of Compositae (Millerieae) in the Galápagos Islands, consists of three morphologically distinct species (Adsersen, 1980). Molecular phylogenetic studies using ITS and *matK* have been completed on this genus (Blöch et al., 2009; Stuessy et al., 2011) along with the larger genus *Melampodium* (40 species) and another small close generic relative, *Acanthospermum* (six species). The results clearly show *Lecocarpus* (and *Acanthospermum*) to be nested within the large and morphologically diverse *Melampodium*. This latter genus is distributed throughout Mexico and Central America, whereas *Acanthospermum* is more concentrated in Central America and northern South America (Blake, 1922). It would not be surprising that *Lecocarpus* might have dispersed from ancestral populations of *Acanthospermum* and diverged rapidly in the oceanic island environment. Species of *Lecocarpus* are woody shrubs with conspicuous white-flowering heads, fruits with wide hoods or long awns, and highly distinctive dissected leaves, quite unlike features known in *Melampodium* or *Acanthospermum*. Because of this striking divergence, and because of the biogeographic hypothesis of origin of *Lecocarpus* from out of *Acanthospermum* (or its immediate ancestor) into the islands, Stuessy et al.

(2011) elected to retain *Lecocarpus* as a separate and, therefore, endemic genus.

The endemic *Sicyocaulis* (Cucurbitaceae), with the single species *S. pentagonus*, has been shown recently from molecular phylogenetic studies involving several nuclear and chloroplast DNA sequences to be nested within the larger genus *Sicyos* (Sebastian et al., 2010). Despite this clear relationship, no suggestion that *Sicyocaulis* should be submerged into *Sicyos*, however, was proposed by the authors. A broad survey of the family has also been completed (Schaefer et al., 2009; Schaefer & Renner, 2011), but *Sicyocaulis* was not included in the samples reported for these analyses.

The endemic *Trigonopterum* (Compositae, Ecliptinae; formerly *Macraea*, nom. illeg.; Wagner & Robinson, 2001), with its single species, *T. laricifolium*, was shown from cpDNA restriction site data (Panero et al., 1999) to be sister to *Sphagneticola* from pantropical coastal areas of Mesoamerica and northern South America. It was earlier regarded as related to the Wedelioid generic complex (Eliasson, 1984).

Hawaiian Islands

This series of isolated islands has long attracted interest of island biologists, in part because of the extremely high level of endemism among angiosperms, ca. 90% at the specific level (Keeley & Funk, 2011). In addition to specific endemism, the archipelago harbors 34 endemic genera of angiosperms (Table 1), the most of any oceanic island system in the world. Furthermore, a comprehensive flora of the archipelago has recently been completed (Wagner et al., 1999), which for the first time has provided a consistent species concept for the many divergent plant lineages. This, in turn, has opened the way for modern investigations on patterns and processes within the endemic flora. A number of molecular phylogenetic studies, therefore, have already been completed on many of the endemic genera.

Despite strong molecular interest in general in the Hawaiian archipelago, four endemic genera have not yet been so investigated, and hence their status remains unchanged. *Dissochondrus* (Gramineae) with its single species, *D. biflorus*, is clearly related to the large genus *Setaria* and "perhaps congeneric" with it (O'Connor, 1999). Molecular studies have surveyed relationships among species of *Setaria* (Kellogg et al., 2009), as well as among genera of Paniceae (Giussani et al., 2001), but neither included samples of *D. biflorus*. It remains, therefore, a distinct endemic genus at this time. *Hibiscadelphus* (Malvaceae) contains seven species that are presumably holophyletic and closely related to *Hibiscus* (Lorence & Wagner, 1995). A morphological cladistic analysis has been completed on relationships among the endemic species but not including representatives of the diversity within *Hibiscus* (Funk & Wagner, 1995). Molecular studies have been completed on relationships among genera of Malvaceae (Pfeil et al., 2002, 2004), but no samples of *Hibiscadelphus* have been included. For the present, therefore, this Hawaiian genus remains endemic. *Neraudia* is a genus of Urticaceae with five closely related species (Wagner et al., 1999). The affinities of *Neraudia* are unclear at this time. Cowan (1949) suggested a tie to *Pouzolsia*. There have been two molecular phylogenetic studies in Urticaceae (Ueda et al., 1997; Monro, 2006), but no samples of *Neraudia* were included. *Touchardia*, also of Urticaceae, is a monospecific genus, suggested by Wagner et al. (1999: 1310) as possibly sharing "a common ancestor with *Urera glabra*." More studies obviously need to be done on these genera. *Urera laciniata* was sampled in a detailed molecular phylogenetic study of Urticaceae using ITS, *trnL-F*, plus morphology (Monro, 2006), but *Touchardia* was not included.

Another genus not investigated at the molecular level, but which has lost its endemic status as a result of morphological studies is *Pelea* (Rutaceae). The genus is nearly endemic to the Hawaiian Islands, with 48 species in the archipelago and only two in the Marquesas (Wagner et al., 1999). Morphological investigations have led to the submergence of *Pelea* into *Melicope* as a distinct section (Hartley & Stone, 1989). In the recent monograph on *Melicope*, Hartley (2001) lists section *Pelea* as consisting of 85 species distributed in Taiwan, Philippines, Borneo, Hawaii, Marquesas, and south to New Caledonia.

A number of other endemic genera in the Hawaiian archipelago have been investigated at the molecular level and shown to be holophyletic; hence, they have retained their endemic status. *Hesperomannia* (Compositae), with three species, used to be considered as being related to South American genera of Mutisieae (Bremer, 1994), but recent molecular phylogenetic studies with chloroplast *ndhF* sequences show affinities to Vernonieae (Kim et al., 1998). More specifically, based on *trnL-F*, *ndhF*, and ITS sequences, the genus remains holophyletic and ties to *Vernonia* from Madagascar and *Gymanthemum* from Africa (Keeley et al., 2007).

The monospecific *Hillebrandia* (Begoniaceae) is morphologically distinct within the family. The more recent and comprehensive molecular phylogenetic studies, using 5.8S, 18S, ITS, and *rbcL* (Clement et

al., 2004) show the genus to be sister to *Begonia* and cladistically basal within the entire family (these are the only two genera). Morphological characters (45) were also added to the ITS (including 26S and 5.8S) data (Forrest et al., 2005), and the branching pattern results for *Hillebrandia* were the same. It is estimated that this ancient lineage should be 51 to 65 million years old, predating the current islands by at least 45 million years, and posing an interesting biogeographic problem. Whether of South Pacific-Malesian or boreotropical origin, this relictual genus remains a distinct island endemic.

Labordia (Loganiaceae) is an endemic genus of 15 species closely related to *Geniostoma* (with 24 species) of the Pacific Basin (Wagner et al., 1999). Conn (1980) submerged *Labordia* into *Geniostoma* as a subgenus, but as Wagner et al. (1999) pointed out, Conn did not study the Hawaiian species. Hence, comprehensive morphological studies, therefore, still remain to be completed. At the molecular level, however, using chloroplast *ndhF* and *rbcL* sequences (Backlund et al., 2000), *Labordia* and *Geniostoma* are sister genera (only one species of each was analyzed, however, *L. tinifolia* and *G. rupestre*). Morphological cladistic analyses have been done among genera of Loganiaceae (Bremer & Struwe, 1992), but *Labordia* was not included. Perhaps most importantly, artificial crosses have been made among eight species of *Labordia* plus *G. rupestre*. All of the species of *Labordia* cross easily with each other (Motley & Carr, 1998), but none with *G. rupestre*. This provided good evidence that the genera should be maintained as distinct (for concurrence see Wood et al., 2007).

Lipochaeta (Compositae, Heliantheae) is traditionally regarded as an endemic genus of 20 species (Gardner, 1979; Wagner et al., 1999). The genus has been divided into two well-marked sections (Gardner, 1979), section *Aphanopappus* (14 species with $2n = 30$ and 5-merous disc florets), and section *Lipochaeta* (six species with $2n = 52$, and with 4-merous disc florets), with a close tie to *Wedelia* being mentioned (Gardner, 1979). Artificial hybridizations (Rabakonandrianina & Carr, 1981) between *Wedelia biflora* ($n = 15$), *W. trilobata* ($n = 28$), four species of section *Lipochaeta*, and six from section *Aphanopappus*, showed a high level of crossability between *W. biflora* and species of section *Aphanopappus* (both are at the same chromosome level), yielding 15II in meiosis, but also nearly sterile. The authors concluded that section *Aphanopappus* must have been derived from *Wedelia* from an ancestor similar to *W. biflora*. Section *Lipochaeta* probably also has come from crosses between two species of *Wedelia*, perhaps also *W. biflora* and an unknown $n = 22$ species (Rabakonandrianina, 1980). Subsequently, *Lipochaeta* sect. *Aphanopappus* has been transferred (Wagner & Robinson, 2001) completely into *Melanthera* (along with the genus *Wollastonia*). *Lipochaeta* as a genus, then, remains endemic to the Hawaiian Islands but with only six species. Molecular phylogenetic studies using cpDNA restriction site data (Panero et al., 1999) have examined intergeneric relationships among genera of subtribe Ecliptinae (Heliantheae), but with only few representatives of the genera here under discussion. *Lipochaeta* ties preferentially to *Wollastonia* (100% BS), but the two species involved, *L. integrifolia* and *Wollastonia biflora* were both later transferred into *Melanthera*, there forming a sister group to another clade that has *M. nivea* at its base. Samples of *Lipochaeta* in the restricted sense were not included. Chumley et al. (2000) published an abstract reporting more detailed molecular phylogenetic studies in these genera using ITS, but as species names for the genera are not given in this brief summary, it is difficult to evaluate the relationships reported.

Nothocestrum (Solanaceae) is an endemic genus of four species (Symon, 1999), earlier considered by Rock (1913) as related to *Athenaea* with seven species from eastern Brazil (Mabberley, 2008). In recent molecular phylogenetic studies of the entire family using *ndhF* and *trnL-F* sequences (Olmstead et al., 2008), *Nothocestrum* (*N. latifolium* and *N. longifolium*) joins in a sister group relationship to the monospecific *Tubocapsicum* (*T. anomalum*) from China. *Nothocestrum* remains an endemic island genus with affinities still uncertain.

Nototrichium (Amaranthaceae) is an endemic genus of three species (Lorence, 1996; Wagner et al., 1999). Hillebrand (1888) believed the generic affinities to lie with *Achyranthes*, and Lorence (1996) concurs. Molecular phylogenetic studies using *matK* (Ogundipe & Chase, 2009), *matK/trnK* (Müller & Borsch, 2005), and *rbcL* (Kadereit et al., 2003) all show a sister relationship with *Achyranthes*. Eliasson (2004) accepts the genus as endemic, and so it remains.

Pteralyxia (Apocynaceae) consists of two species, one restricted to Kauai (*P. kauaiensis*) and the other to Oahu (*P. macrocarpa*). Here again, the affinities of this genus are not terribly clear, perhaps with *Vallesia*, a tropical American genus of five species into which Hillebrand (1888) first described *P. macrocarpa* (as *V. macrocarpa*). Molecular phylogenetic analyses (Livshultz et al., 2007) using chloroplast regions (*trnL* intron, *trnL-F* spacer, *rpl16* intron, *rps16* intron, *matK*, and 3′ half of the *trnK* intron), plus 16 morphological characters, revealed *Pteralyx-*

ia (*P. kauaiensis*) to be sister to *Alyxia* (four species analyzed out of more than 100). These two genera were sister to *Plectaneia thouarsii*. Pollen studies by van der Ham et al. (2001) showed a close resemblance between *Pteralyxia* and *Alyxia*. *Pteralyxia* remains as an endemic genus at this time.

Schiedea (Caryophyllaceae) is a large endemic genus of 34 species (32 extant; Willyard et al., 2011), presumably having been derived (along with the related *Alsinodendron*) from an ancestor similar to *Arenaria*. A number of studies have been done on this large endemic complex of species (e.g., Wagner et al., 1995, 1999; Soltis et al., 1996; Weller et al., 2001; Kapralov & Filatov, 2006; Sakai et al., 2006). Much of the previous work is summarized in a recent monograph of the genus (Wagner et al., 2005). As shown in this treatment, with molecular phylogenetic analyses using nr ITS and ETS regions, plus morphology, *Schiedea* is holophyletic and highly supported (96% BS). The sister group consists of *Honckenya peploides* and *Wilhelmsia physodes*. Further molecular phylogenetic investigations by Willyard et al. (2011), using eight plastid and three low-copy nuclear markers, confirm these points as well as providing support for holophyly ("monophyly") of the many species. In context of the present study, there seems no doubt that *Schiedea* remains an endemic genus.

The two largest adaptively radiating generic complexes in Hawaii, the silverswords and lobeliads, have been investigated at the molecular level, and both are now known to contain different types of topological phylogenetic relationships. One dramatic example of evolution of endemic genera in oceanic islands is found in the silversword alliance of 28 species, consisting of *Argyroxiphium*, *Dubautia*, and *Wilkesia* (Compositae, Madieae). The three genera are nested as a holophyletic group within the other genera of Madiinae (Baldwin, 2003). A molecular analysis (ITS) among all species of the three genera reveals *Argyroxiphium* and *Dubautia* to be clearly holophyletic, but *Wilkesia* is derived from out of *Dubautia*, tying in a clade with *D. paleata*, *D. raillardioides*, and *D. latifolia*. Despite this topological position, so far no effort has been made to submerge *Wilkesia* formally into *Dubautia*, perhaps due to the extreme morphological divergence of the former (Carr, 1985) and its high conservation visibility.

The Hawaiian lobeliads are a huge holophyletic assemblage of ca. 126 species (Givnish et al., 2009), the largest adaptively radiated group on any oceanic island. Among the endemic genera are *Brighamia*, *Clermontia*, *Cyanea*, *Delissea*, *Rollandia*, and *Trematolobelia*. *Trematolobelia*, with four species, is shown from seven chloroplast regions to be sister to *Lobelia* sect. *Galeatella*, also nested among other endemic species of *Lobelia*. In a recent revision of *Trematolobelia*, Lammers (2009) points to this topological result and concludes that deciding on the proper status of this endemic genus must wait until the larger genus, *Lobelia*, can be carefully investigated and taxonomically evaluated. At present, therefore, *Trematolobelia* remains an endemic genus in the archipelago. Based on all molecular phylogenetic studies to date with chloroplast sequences (Givnish et al., 1995, 2009; Givnish, 1998; Antonelli, 2008), *Cyanea* and *Clermontia* are both holophyletic and sister to each other. Likewise, *Brighamia* and *Delissea* are sister taxa and both also holophyletic. These genera, therefore, retain their endemic island status. *Rollandia* has been recognized as a distinct endemic genus with eight species (Lammers, 1999; Wagner et al., 1999). Molecular phylogenetic studies, however, using chloroplast restriction site data (Givnish et al., 1995) reveal *Rollandia* to be a holophyletic unit but nested within *Cyanea*. As a result of the early availability of these data, Lammers et al. (1993) merged *Rollandia* into *Cyanea*, emphasizing that there is only one morphological feature that defines the former: the adnation of the staminal column to the corolla. In the face of molecular data, this was judged no longer sufficient to support generic recognition. *Rollandia*, therefore, disappeared as an endemic genus.

Munroidendron (Araliaceae) is a monospecific endemic genus closely related to, and possibly derived from, *Tetraplasandra* (also endemic with seven species; Lowry & Wood, 2000), *Reynoldsia* (six species, Samoa, Marquesas, Society Islands, one in Hawaii [*R. sandwicensis*]; Lowry, 1999), or *Gastonia* (11 species from eastern Africa, Malesia, and the Indian Ocean islands; Philipson, 1970). Relationships among these genera were studied at the molecular level by Costello and Motley (2001) using ITS1 and 2 and the non-transcribed spacer of nr 5S. *Tetraplasandra* is seen as holophyletic and substantiated as a good genus. The one species of *Gastonia* included, *G. rodriguesiana*, was designated as the outgroup and remains apart. *Munroidendron* (*M. racemosum*), however, ties as sister to *R. sandwicensis*, but only two of the six species were analyzed (the other being *R. verrucosa*). *Reynoldsia verrucosa* is the sister taxon to all other species of *Tetraplasandra* and *R. sandwicensis* and *M. racemosum*. The results suggested that most Hawaiian members of this complex are holophyletic, but with *Reynoldsia* showing "apparent paraphyly." This hesitation was

due to the limited sample of only two out of six species of the genus being analyzed plus some incongruence between trees for ITS and 5S-NTS. Costello and Motley (2001) suggested that all three genera could be combined into one genus, or alternatively, *R. sandwicensis* might be combined into *Munroidendron*. These same authors (Costello & Motley, 2007) again examined relationships among these genera using ITS, 5S-NTS, plus morphology (39 morphological and anatomical features), increasing the sample to include all species of *Tetraplasandra* (except for *T. lydgatei*), *Reynoldsia*, *Munroidendron*, and three species (four with morphological data) of *Gastonia*. With molecular data, *Munroidendron* ties again sister to *R. sandwicensis* with high (100% BS) support. With morphological data only, *Munroidendron* joins in a polytomy with all species of *Tetraplasandra*. The authors again sketch taxonomic alternatives to deal with these results, but the one they "prefer" is to treat as a separate genus the non-Hawaiian species of *Reynoldsia*, and *R. sandwicensis* and *Munroidendron* together as a single genus. This being the case, *Munroidendron* would become bispecific but still remain as an endemic genus. In parallel, however, Plunkett and Lowry (with associates) have examined broad generic relationships among genera of Araliaceae based on ITS (Plunkett et al., 2001), with *trnL-F* (Plunkett et al., 2004a, 2004b), and these also combined with ETS (Plunkett & Lowry, 2010). All results are summarized in Lowry and Plunkett (2010). The taxonomic approach they have taken has been to maximize holophyly and minimize nomenclatural change, which led to a very broad concept of the genus *Polyscias* to include *Munroidendron*, *Reynoldsia*, plus other taxa, in *Polyscias* subg. *Cuphocarpus*. *Munroidendron*, therefore, disappears from the endemic genera of the islands.

Some recent molecular phylogenetic investigations in the Hawaiian archipelago have provided inconclusive results regarding relationships, based mainly on limited sampling, and the genera, therefore, are still considered endemic. *Bobea* (Rubiaceae, Guettardeae), with four species, is shown with ITS sequences to be sister to *Guettarda* (Achille et al., 2006). Five chloroplast sequence regions (Bremer & Eriksson, 2009) were not particularly helpful for resolving intergeneric relationships among *Bobea* and 13 other genera. Darwin and Chaw (1999) suggested that on morphological grounds *Bobea* is "closely related to *Timonius* DC." *Kokia*, another endemic genus of Malvaceae, consists of four species of unclear generic affinities (Bates, 1999). Morphological relationships among the species have been analyzed by Funk and Wagner (1995). Generic affinities have been suggested to be with *Thespesia* and the segregate *Cephalohibiscus* (Fryxell, 1979; Funk & Wagner, 1995). Molecular studies using *K. drynarioides* only, with *ndhF* sequences (plus 11 morphological features; Pfeil et al., 2002) and in another study combined with ITS sequences (Seelanan et al., 1997), all reveal a strong tie as a sister group (99% BS) with the genus *Gossypioides* (*G. kirkii*), consisting of two species from tropical Africa and Madagascar (Mabberley, 2008). Species from these two genera were used as outgroups to root a low-copy number gene analysis of *Gossypium* (Álvarez et al., 2005), but this provided no additional insights on affinities of *Kokia*. *Remya* (Compositae, Astereae) is an endemic genus consisting of three species, presumably related to the large (ca. 100 species) Australasian *Olearia* (Wagner & Herbst, 1987). The only molecular phylogenetic study of *Remya* and relatives is by Karaman-Castro and Urbatsch (2009) using ITS sequences. Overall resolution, however, is poor, only showing *R. kauaiensis* and *R. mauiensis* to be holophyletic (100% BS) and placed in the "Austral Grade" with representatives of *Olearia* and 13 other genera.

In several other cases in the Hawaiian Islands, molecular investigations have shown endemic genera to be nested within continental progenitors, hence making the latter paraphyletic, but the authors in these cases have not yet taken formal taxonomic action. This same situation was described above in the endemic silversword genus *Wilkesia* (Compositae) that clearly nests within *Dubautia* (also endemic).

Broussaisia is the only species of Hydrangeaceae in the Hawaiian Islands, and it represents an endemic genus. It has an unusual berry-like fruit, an almost inferior ovary, styles that are connate (these features from Wagner, 1999), and is also polygamo-dioecious (Samain et al., 2010). It was suggested (Fosberg, 1939; Wagner et al., 1999) to be related to *Dichroa*, which has 12 species in Asia and Malesia (Mabberley, 2008). Molecular phylogenetic studies using *rbcL* (Soltis et al., 1995) and *rbcL* combined with *matK* and morphology (Hufford et al., 2001) show *Broussaisia* to nest with species of *Hydrangea* (and *Dichroa*). With five chloroplast regions (Samain et al., 2010), *B. arguta* is nested within *Hydrangea* and distinct from *Dichroa*, which also falls within *Hydrangea*. The authors conclude that "inclusion [in *Hydrangea*] of these genera [and six others] is suggested" (p. 598), but no formal action was taken. Even more recent investigations with six cpDNA regions (Xiang et al., 2011) show *Broussaisia* as sister

to a clade containing six other genera plus five other species of *Hydrangea*.

Isodendrion (Violaceae) is an endemic genus of four species, but one is already extinct and three are considered rare (Wagner et al., 1999). Morphological and cytological data give suggestions that the genus may be related to *Hymenanthera* and *Melicytus*. Molecular phylogenetic studies in Violaceae, using *rbcL*, *atpB*, *matK*, and 18S rDNA (Tokuoka, 2008), and with *I. laurifolium* and *I. longifolium*, show them nested within *Hybanthus*; however, no taxonomic changes were suggested by the author.

Platydesma (Rutaceae) is an endemic genus of four species with obscure generic affinities based on morphology (Stone et al., 1999). Molecular phylogenetic studies using ITS sequences (Harbaugh et al., 2009) show *P. rostrata* and *P. spathulata* to be nested in the center of *Melicope*, but sister to all the endemic Hawaiian species sampled, all formerly in *Pelea*. *Platydesma*, however, is hermaphroditic and morphologically divergent and has not been included in *Melicope* by Hartley (2001). It remains an endemic genus at this time.

Two endemic genera of Labiatae occur in Hawaii, *Haplostachys* with five species and *Stenogyne* with 20 species. A third genus, *Phyllostegia*, is nearly endemic with 32 species restricted to Hawaii (Wagner et al., 1999) and only one in Tahiti (*P. tahitensis*). All three genera belong to subfamily Stachydeae (Scheen et al., 2010). Molecular phylogenetic studies using *rbcL* and *trnL* intron, plus the nr 5S non-transcribed spacer region (Lindqvist & Albert, 2002; Lindqvist et al., 2003), have shown all three genera to be holophyletic, individually and as a complex, but all nested within *Stachys*, particularly close to relatives of the Pacific Coast of North America (Baldwin & Wagner, 2010). The Hawaiian complex appears highly derived, being in the uppermost clade of *Stachys*. Lindqvist and Albert (2002) suggest transfer of the three genera into *Stachys*, but they point out that specific epithets already exist in *Stachys* in the case of two species of *Haplostachys*, 16 of *Phyllostegia*, and eight of *Stenogyne*, which would require considerable nomenclatural changes. This is an excellent example of the basic problem that this present paper addresses. To eliminate paraphyly in *Stachys* requires that the authors submerge the island genera, which they would prefer to do, but the morphological distinctness of these genera, plus concern about changes of specific epithets, has caused them to hesitate. Further studies on relationships among these genera are obviously also needed.

Finally, a few molecular studies have shown progenitors to be paraphyletic, which has led to formal taxonomic action and loss of endemic status for the island genus. *Rollandia* (Campanulaceae) was one such case discussed above. Another case is *Alsinodendron* (Caryophyllaceae), recently treated as an endemic genus of four species (Wagner et al., 1999), but clearly related to *Schiedea*. Molecular phylogenetic studies (ITS and ETS, plus morphology), summarized in Wagner et al. (2005), show *Alsinodendron* to be nested within *Schiedea* as a holophyletic clade sister to *S. verticillata*. *Alsinodendron* is now viewed as making up two sections of *Schiedea*, *S. obovata* and *S. trinervis* forming section *Alsinodendron* and *S. viscosa* and *S. lychnoides* constituting section *Nothoschiedea*. It should be mentioned that artificial hybridizations have been successful between the two genera, but this is not necessarily unusual among genera of holophyletic alliances in oceanic islands (e.g., also among the silversword genera; Carr, 1995).

Madeiran Islands

The Madeiran archipelago consists of the largest island Madeira (725 km^2), plus Porto Santo and the Desertas, all more than 950 km west of Portugal in the eastern Atlantic Ocean. Madeira itself contains 1163 vascular plants, of which 113 (10%) are endemics (Press & Short, 1994), the same percentage also prevailing within the entire archipelago. Among the endemics in the archipelago are five endemic genera: *Chamaemeles* (Rosaceae, one species), *Monizia* (Umbelliferae, one species), *Musschia* (Campanulaceae, two species), *Parafestuca* (Gramineae, one species), and *Sinapidendron* (Cruciferae, four species).

Three endemic taxa continue to be regarded as good genera. *Chamaemeles*, represented by the sole species *C. coriacea*, is endemic to Madeira, Porto Santo, and Deserta Grande (plus on the small Doca Island nearby). Affinities of this genus are obscure (Press & Short, 1994), and no molecular investigations have to date been completed on the taxon. *Monizia* is also a monospecific genus endemic to Madeira and Deserta Grande (as well as on Selvagen Grande, of the Salvage Islands, located 300 km south of Madeira). Molecular phylogenetic studies (Downie et al., 2001), especially ITS sequences (Spalik & Downie, 2007), have continued to support its recognition as a distinct genus endemic to the archipelago. *Sinapidendron* is an endemic genus with three species confined to Madeira and one (*S. sempervivifolium*) to Deserta Grande in the Desertas Islands. *Sinapidendron angustifolium* and *S. frutes-*

cens have been included in a molecular phylogenetic study of tribe Brassiceae using ITS and *trnL* intron sequences (Warwick & Sauder, 2005), forming a highly supported (99% BS) trichotomy with *Erucastrum varium* in ITS and identity with *Diplotaxis assurgens* with *trnL*. With combined data, the two species of *Sinapidendron* form a holophyletic group, sister to *D. siifolia*. Earlier cpDNA restriction site data (Warwick & Black, 1993) for many of the same taxa also revealed *Sinapidendron* to be holophyletic.

Two endemic genera of the Madeiran archipelago, however, have been discovered to be nested within larger genera of continental regions. *Musschia* is an endemic genus confined to Madeira and Deserta Grande (plus Doca Islet). Both species are considered rare (Press & Short, 1994). Roquet et al. (2008) completed a broad survey of genera in Campanulaceae using ITS and *trnL-trnF*, and *M. aurea* was included in the analyses. Combined data gave good resolution in which *Musschia* ties with 100% BS support to *Campanula peregrina* and *C. primulifolia*. Called the "Musschia clade," the authors favored placing this and two other main clades within *Campanula*, but they emphasized the need for further investigations before such a decision might be taken (and combinations actually made). *Parafestuca* is a monospecific endemic genus confined to eastern and central Madeira. A morphological reexamination and new chromosome data suggested inclusion of this genus into *Koeleria*, and this has been further supported by nr TS and cp *trnT-F* sequences in this same investigation (Quintanar et al., 2006). Within tribes Aveneae and Poeae, *P. albida* ties best with species of *Koeleria* in the well-supported (99% BS) Koelerinae clade. A new combination has been formally made, but due to the specific epithet being occupied already in *Koeleria*, the new name *K. loweana* has been proposed. *Parafestuca* disappears, then, as an endemic genus in Madeira.

Robinson Crusoe Islands

Of 73 total angiosperm genera occurring in the Robinson Crusoe archipelago (Marticorena et al., 1998), 12 are regarded as endemic (Table 1), which yields a relatively high 16% level of generic endemism. Three of these genera, two of them monotypic, have not yet been examined with modern techniques and interpretations, and, therefore, remain accepted as good genera at the present time. *Juania* (Palmae) is scarce on Masatierra Island, being found scattered on the highest ridges (Stuessy et al., 1983). Several pre-molecular studies were done on aspects of morphology and anatomy of *J. australis* (Moore, 1969; Tomlinson, 1969; Uhl, 1969), but the generic affinities were not precisely determined. *Selkirkia* is a monospecific, endemic genus of Boraginaceae, and the family has recently had molecular attention (e.g., Långström & Chase, 2002). *Selkirkia*, however, was not included in the samples and analyses, perhaps due to its extreme rarity. *Megalachne* (Gramineae) consists of two endemic species, *M. berteroana* and *M. masafuerana*, both of which occur on both major islands of the archipelago (Baeza et al., 2002). The genus has at times been included within *Bromus* (Pilger, 1920; Skottsberg, 1921, 1953), but more recently it has been regarded as distinct but close to *Bromus* and *Festuca* (Matthei, 1986; Watson & Dallwitz, 1992) or *Metcalfia* and *Podophorus* (Soreng et al., 2001). Molecular studies have been done on *Bromus* (Saarela et al., 2007), but neither species of *Megalachne* was included.

The poorly known monospecific endemic genus *Yunquea* (Compositae, Cardueae) has recently been regarded as synonymous with *Centaurodendron* (Susanna & Garcia-Jacas, 2001) based on limited morphological data, but this species, known only from the virtually inaccessible peak El Yunque on Masatierra Island, has not been studied in any meaningful way, morphological or otherwise. Molecular surveys of subtribe Centaureinae have been accomplished (Garcia-Jacas et al., 2001; Susanna et al., 2011), but *Yunquea* has not been included.

Two genera have been investigated recently and submerged into other genera based primarily on other than molecular data. Based on morphological analyses, the monospecific genus *Rhetinodendron* (Compositae, Senecioneae; *R. berteroi*) was included into the larger endemic genus *Robinsonia* by Pacheco et al. (1985) but retained at the subgeneric level (Sanders et al., 1987). Subsequent ITS sequence studies (Sang et al., 1995) supported this taxonomic configuration. However, even more recent ITS studies, using a larger sample of species in the close continental relative *Senecio* (Pelser et al., 2007, 2010b), question this conclusion and suggest that *R. berteroi* might be more closely related to another group of species of *Senecio* in South America. Six combined chloroplast sequences (*trnL-trnL-F*, *psbA-trnH*, 3′*trnK*, 5′*trnK*, *ndhF*, and *psbJ-petA*) used by the same authors, however, show the genus to be holophyletic. Unfortunately, this all becomes sadly academic as introduced rats have destroyed the last known living specimen, and *R. berteroi* is now presumed extinct (Danton & Perrier, 2005).

Other genera have been investigated at the molecular level, and they remain acceptable in a cladistic context at this point. *Cuminia* (Labiatae)

with two species, based on *trnL/F* and ITS sequences, appears a good genus related to *Monardella* and *Minthostachys* (Trusty et al., 2004) or more broadly to the New World *Clinopodium* group (Bräuchler et al., 2010). The hybrid ×*Margyracaena* (Rosaceae) exists as a stabilized vegetatively reproducing intergeneric hybrid (as ×*M. skottsbergii*) between the native *M. digynus* and the introduced *Acaena argentea*, its origin documented by RAPD markers (Crawford et al., 1993). Its hybrid origin is likely to have occurred during historical times.

Two endemic genera, *Dendroseris* and *Robinsonia* (Compositae), have been shown to be nested within larger continental progenitors. *Dendroseris* is the largest endemic genus in the archipelago with 11 species. A member of the dandelion tribe, Lactuceae, it is a group of striking rosette trees 3–5 m tall, which many years ago were recognized as a distinct genus (Don, 1832). Divergence within the complex, however, is dramatic, such that Skottsberg at one point (1953) elected to recognize four genera within the complex. These species are now treated as belonging to three subgenera within one genus (Sanders et al., 1987), but there is no question that there is much morphological diversity. Molecular sequence studies using nrITS (Sang et al., 1994) have suggested *Dendroseris* to be holophyletic. This early result was confirmed by a much-expanded database and sampling within subtribe Sonchinae using ITS and chloroplast *matK* sequences (Kim et al., 2007). In this study *Dendroseris* was shown to be nested within the diverse and widespread genus *Sonchus*. Acting on these results, recently Mejías and Kim (2012) have made the formal combinations into *Sonchus*. Because many of the specific epithets in *Dendroseris* also exist within the large genus *Sonchus*, this required new names for five species. If this taxonomic perspective is adopted, then the largest endemic genus in the island disappears. The species, obviously, still remain endemic at the specific level.

The second largest genus of Compositae in the archipelago is *Robinsonia* (Senecioneae) with seven endemic species (including *R. berteroi*, originally in *Rhetinodendron* mentioned above). Molecular phylogenetic studies (Pelser et al., 2007, 2010a) have shown this genus to nest clearly within the very large *Senecio* that has more than 200 species in continental Chile alone (Cabrera, 1949) and perhaps 1200 throughout the world (Nordenstam, 2007). On the basis of these results, Pelser et al. (2010b) combined *Robinsonia* formally into *Senecio*. Due to so many epithets already pre-empted within the larger *Senecio*, four new names have been created. On the morphological level, *Robinsonia* is quite distinct in being a series of rosette dioecious woody trees 0.5–3 m tall.

Molecular investigations of *Centaurodendron*, another endemic genus of Compositae (Cardueae) with two species in the islands, using combined ITS, ETS, and plastid *trnL-trnL-F*, *rpl32-trnL*, and *ndhF* (Susanna et al., 2011), show it (*C. palmiforme* analyzed) to be nested within the broadly disjunct *Plectocephalus* (occurring in Ethiopia, North America, and South America) along with the South American *Centaurea cachinalensis* and *C. floccosa*. Despite this topological position, which renders *Plectocephalus* paraphyletic, Susanna et al. (2011) have retained *Centaurodendron* as an endemic genus with arguments for doing so based on morphological distinctness. This is the only example, of which we are aware, whereby the authors have taken such an explicit stand (cf. discussion on Susanna et al., 2011: 268–270).

Perhaps the most interesting genus in the archipelago is *Lactoris* (Lactoridaceae, consisting of *L. fernandeziana*), not only being an endemic genus, but also an endemic family, the only family of flowering plants restricted to a single oceanic island. Therefore, *Lactoris* has a double importance in conservation at both generic and familial levels, and it has been used as a rallying focus for plant conservation in the islands. There are perhaps 1000 plants existing on the higher difficult-of-access regions of Masatierra (Robinson Crusoe) Island (Crawford et al., 1994, 2001). Molecular sequence studies have shown *Lactoris* to nest within Aristolochiaceae near *Aristolochia* based on *rbcL* (Qiu et al., 1993), 18S rDNA (Soltis et al., 1997), and a 17-gene analysis (Soltis et al., 2011). If one were to accept these data and analyses and act on strict holophyly, the family Lactoridaceae would disappear from the island (and the world). The branch lengths involved with the phylogenetic reconstructions are very long, however, and this leaves some doubt as to the actual affinities of this genus (Stuessy et al., 1998). Additional molecular phylogenetic investigations (Wanke et al., 2006) using the chloroplastic *matK* and *trnK* show *Lactoris* to be the sister group to all other sampled Aristolochiaceae. Morphologically the family is quite distinct in its trimerous floral symmetry, zig-zag branching, and tetrad pollen (Zavada & Taylor, 1986; Sampson, 1995). A reasonable perspective at this time seems to be to retain *Lactoris* in a separate family but indicate a close relationship to Aristolochiaceae. It clearly belongs in Aristolochiales or Piperales, a position that is supported also by morphological and anatom-

ical data (Carlquist, 1990, 1992; Tobe et al., 1993; Tucker & Douglas, 1996; González & Rudall, 2001).

Somewhat surprisingly, a new endemic genus, *Nothomyrcia* (Myrtaceae), has just been added to the archipelago based on molecular phylogenetic studies. This genus, with its sole species, *N. fernandeziana*, is the dominant forest tree on Masatierra (Robinson Crusoe) Island and was previously included within *Myrceugenia*. Another endemic species of this genus, *M. schulzii*, also occurs in the archipelago but on the younger island of Masafuera. Recent molecular phylogenetic studies based on ITS, ETS, and four chloroplast markers (partial *trnK-matK*, *rpl32-trnL*, *trnQ-5′rps16*, and *rpl16*; Murillo-A. et al., 2012) have shown that *Myrceugenia fernandeziana* is very genetically divergent and falls outside all other known genera of Myrteae, being nearest to *Blepharocalyx*. If one acts taxonomically from these new data, a separate genus should be recognized under the existing name *Nothomyrcia* (Murillo-Aldana & Ruiz, 2011). This, then, represents a new endemic genus in the archipelago based on the new molecular data—a surprising reverse trend! It must be cautioned, however, that the most recent monographer of *Myrceugenia*, Landrum (1981a, 1981b), is not convinced that separate generic status for *M. fernandeziana* is warranted at this time based on morphological considerations (pers. comm.).

St. Helena

This single island of 121 km² sits in the South Atlantic Ocean some 1931 km west of the African continent. Due to this isolation, 49 endemic species of ferns and angiosperms have developed within a total flora of 320 species (Cronk, 2000). Among these occur 10 endemic flowering plant genera (all but two being monospecific): *Mellissia* (Solanaceae), *Nesiota* (Rhamnaceae), *Nesohedyotis* (Rubiaceae), *Trimeris* (Campanulaceae), and *Trochetiopsis* (Sterculiaceae, three species), plus five endemic genera of Compositae, *Lachanodes* and *Pladaroxylon* (Senecioneae), *Melanodendron* and *Commidendrum* (Astereae, the latter with four species), and *Petrobium* (Coreopsideae).

Several genera endemic to St. Helena have not yet been investigated molecularly, and for these, no change of status has been recommended. Lacking modern studies are *Nesiota* and *Trochetiopsis*, the latter with three species that sadly are now extinct in the wild (Cronk, 2000). Relationships among genera of Sterculiaceae have been examined with molecular data (Alverson et al., 1999; Wilkie et al., 2006), but the rare *Trochetiopsis* was not included.

Other genera have been investigated with new molecular markers, but no change in generic status has been suggested. *Mellissia* was submerged by Hunziker (1995, 2001) into *Withania* based on morphology. Molecular data with cp *ndhF* and *trnL-F* (Olmstead et al., 2008) suggest *M. begoniifolia* as sister to two species of *Withania*. *Mellissia*, therefore, is still regarded as a good endemic genus, and Fay et al. (2007) concur. The monospecific *Nesohedyotis* (*N. arborea*) was analyzed with up to five chloroplast regions (*rbcL*, *trnT-F*, *rps16*, *atpB-rbcL*, and *ndhF*) in a broad survey of subfamily Rubieae, tribe Spermacoceae (Bremer & Eriksson, 2009), and it falls in a large unresolved polytomy with representatives of 10 other genera of Rubioideae (such as *Mitracarpus*, *Psyllocarpus*, etc.). A survey using four chloroplast (*atpB-rbcL*, *petD*, *rps16*, and *trnL-F*) and two nuclear (ITS and 5S-NTS) DNA regions (Kårehed et al., 2008) within Spermacoceae revealed *Nesohedyotis* as sister (and basal) to *Oldenlandia tenuis* and *O. salzmannii* and the "Spermacoce clade," but this position received only weak support. In another analysis of three chloroplast sequences (*atpB-rbcL*, *rps16*, and *trnL-trnF*) in tribe Spermacoceae (Groeninckx et al., 2009), *Nesohedyotis* ties as sister to *Emmeorhiza*. With regard to *Petrobium*, Stuessy (1988) suggested placement into *Bidens*, but the molecular (ITS) data (Kimball & Crawford, 2004) do not support this. Ryding and Bremer (1992) were likewise against such a transfer on morphological and cladistic grounds. *Lachanodes* was submerged based on morphology into *Senecio* by Mabberley (1975), but molecular studies by Pelser et al. (2010a) using ITS/ETS and *ndhF*, *psbA-trnH*, 5′ and 3′*trnK*, and *trnL-F* intergenic spacers, regard it still as a good genus (as did Cronk, 2000). *Pladaroxylon* was very early placed as a section within *Lachanodes* (Endlicher, 1838), but Pelser et al. (2010a) treat the former as an independent genus. Mabberley (1975) also submerged *Pladaroxylon* into *Senecio*, but Jeffrey (1979) accepted the two genera.

New investigations in some cases have resulted in suggestions for change in generic status. *Melanodendron* and *Commidendrum* have been examined with molecular sequences (with ITS 1 and 2; Eastwood et al., 2004), and the phylogeny does "weakly suggest" that both "may be nested" (p. 81) within *Felicia*. The authors, however, believe that more sampling is required in *Felicia* and *Amellus* before relationships of the endemic island genera can be satisfactorily determined. The two genera are clearly related to each other in morphological and anatomical features (Cronk, 1987; Carlquist, 2001). *Trimeris* has been placed recently by Lammers (2011) into *Lobelia* (as

section *Trimeris*) based on morphological evidence, primarily due to his preference for keeping the latter genus large and not fragmented into many smaller, segregate genera. If recognized, these small genera would require many accompanying nomenclatural changes at the specific level. Molecular studies have been completed on Campanulaceae subfam. Lobelioideae (Antonelli, 2008) using *rbcL*, *ndhF*, and the *trnL-F* region, but *Trimeris* (i.e., as *L. suaevolifolia*) was not included.

Impact of New Data on Status of Genera Endemic to Oceanic Islands

The new analyses have led to several actions that impact taxonomic status of endemic genera in oceanic islands (Table 3). First, despite new investigations, the genera may still be recognized (i.e., a sister-group relationship is revealed causing no challenges to holophyly), in which case no taxonomic change has been instituted. Second, the genera may have been submerged already based on recent non-cladistic (or non-molecular) data and syntheses. Third, the genera have been revealed to be nested within a larger parental genus based on molecular phylogenetic studies. If this has happened, then the authors have acted on the information in one of three ways: (1) the genera are still recognized (i.e., no taxonomic modification); (2) the genera are submerged into the parental genera (or recommended that this be done) but without nomenclatural combinations being presented; or (3) the genera are submerged and combinations made formally. It is this last action, obviously, that truly eliminates the genera as endemic in the island or archipelago and creates an impact on conservation. These are taxonomic perspectives, of course, and no one is absolutely compelled to follow them. Furthermore, the taxa remain endemic species but not at the generic level.

Taking the detailed results from Table 3, we summarize in Table 4 the general impact of new data (especially molecular) and the cladistic interpretations on generic limits in oceanic islands. Sixty-four endemic genera continue to be accepted, mostly because they appear distinct (sister-group relationships) and not nested within any other genus. Seven genera have in recent years already been submerged based on non-molecular data and/or non-cladistic methods. A total of 29 genera have now been shown to nest within larger parental genera, the former of which would all disappear should concepts of absolute holophyly be applied. However, there is clearly some hesitation to eliminate some of these endemic genera as 15 are still recognized by the investigating authors. Six genera have been stated to belong more properly within the larger parents, but no formal transfers have yet been made. Finally, eight genera have disappeared from the ranks of island endemics by being combined into their parental stocks. It is important to remember, however, that there is no *absolute* requirement to submerge endemic island genera, no matter what the prevailing taxonomic or evolutionary context might be.

The overall impact of application of strict holophyly to avoid paraphyly for concepts of genera in oceanic islands is summarized in Table 5. The amount of change varies among island groups ranging from 29% to 43% (ignoring the Bonin Islands). The percent change in numbers of recognized endemic genera in the several oceanic islands/archipelagos examined would be 32% if all authors were to act taxonomically (and nomenclaturally) on the basis of classification using strict holophyly. That is, nearly one third of angiosperm genera endemic to these oceanic islands/archipelagos would disappear.

Perspectives on Holophyly and Paraphyly with Endemic Genera of Oceanic Islands

The problem of circumscription of genera in oceanic islands is simply one particular case of the challenge of recognizing genera worldwide (e.g., Barrett et al., 2005). There have been four basic approaches to delimiting genera during the past two or more centuries. First, a genus is recognized by divergence in characters, usually morphological, but supported and aided by other data from anatomy, embryology, palynology, cytology, DNA, and so on. Important in these comparisons is to seek gaps in character divergence such that species are grouped into genera based on characters they share with each other and that are not present in other species (or present to a different degree). Second, often ecological differences are used, based on geography, ecology, or both. The idea is that a genus may have entered a different adaptive environment or achieved a different adaptive norm from other groups of species. Widespread dispersal, obviously, can blur such distinctions. Third, genera usually do not cross easily with each other. This is a complex matter and usually not all species between two or more genera have been crossed either naturally or artificially, but in general, genera should cross with much more difficulty than should species. There is no cross known between families of angiosperms (Stuessy, 2009). Fourth, in a cladistic context, genera must be supported by synapomorphies (as with all taxa recognized in cladistic classification), and they must be holophyletic.

Table 3. Impact of molecular phylogenetic (or other evolutionary) studies on the taxonomic status of endemic genera of angiosperms in selected oceanic islands or archipelagos. Based on data in Ono and Kobayashi (1985), Wiggins and Porter (1971), Hansen and Sunding (1993), Press and Short (1994), Marticorena et al. (1998), Wagner et al. (1999), Cronk (2000), Danton et al. (2006), plus additional recent articles (cf. Table 2).

		Based on molecular phylogenetic studies, genus nested within a larger parental genus		
Genus still accepted	Genus submerged based on non-cladistic results	Genus still recognized	Genus submerged into parent (without combinations)	Genus submerged with combinations
Bonin Islands				
Dendrocacalia	*Boninia* (in *Melicope*)			
Canary Islands				
Aeonium *Aichryson* *Allagopappus* *Argyranthemum* *Bencomia* *Bethencourtia* *Bystropogon* *Dendriopoterium* *Dicheranthus* *Gesnouinia* *Gonospermum* *Ixanthus* *Kunkeliella* *Marcetella* *Monanthes* *Parolinia* *Schizogyne* *Spartocytisus* *Todaroa* *Vieraea*	*Heywoodiella* (in *Hypochaeris*) *Neochamaelea* (in *Cneorum*)		*Atalanthus* (as *Taeckholmia*) (in *Sonchus*) *Babcockia* (in *Sonchus*) *Greenovia* (in *Aeonium*) *Lactucosonchus* (in *Sonchus*) *Lugoa* (in *Gonospermum*) *Sventenia* (in *Sonchus*)	*Tinguarra* (in *Athamanta*) *Plocama**
Galápagos Islands				
Brachycereus *Jasminocereus* *Scalesia* *Trigonopterum*		*Darwiniothamnus* (in *Erigeron*) *Lecocarpus* (in *Melampodium*) *Sicyocaulis* (in *Sicyos*)		
Hawaiian Islands				
Argyroxiphium *Bobea* *Brighamia* *Clermontia* *Cyanea* *Delissea* *Dissochondrus* *Dubautia* *Hesperomannia* *Hibiscadelphus* *Hillebrandia* *Kokia* *Labordia* *Lipochaeta* *Neraudia* *Nothocestrum* *Nototrichium* *Pteralyxia* *Remya* *Schiedea* *Tetraplasandra* *Touchardia*	*Pelea* (in *Melicope*)	*Broussaisia* (in *Hydrangea*) *Haplostachys* (in *Stachys*) *Isodendrion* (in *Hybanthus*) *Phyllostegia* (in *Stachys*) *Platydesma* (in *Melicope*) *Stenogyne* (in *Stachys*) *Trematolobelia* (in *Lobelia*) *Wilkesia* (in *Dubautia*)		*Alsinodendron* (in *Schiedea*) *Munroidendron* (in *Polyscias*) *Rollandia* (in *Cyanea*)
Madeiran Islands				
Chamaemeles *Monizia* *Sinapidendron*		*Musschia* (in *Campanula*)		*Parafestuca* (in *Koeleria*)
Robinson Crusoe Islands				
Cuminia *Juania* *Lactoris* ×*Margyracaena* *Megalachne* *Nothomyrcia* *Selkirkia*	*Rhetinodendron* (in *Robinsonia*) *Yunquea* (in *Centaurodendron*)	*Centaurodendron* (in *Plectocephalus*)		*Dendroseris* (in *Sonchus*) *Robinsonia* (in *Senecio*)
St. Helena				
Lachanodes *Mellissia* *Nesiota* *Nesohedyotis* *Petrobium* *Pladaroxylon* *Trochetiopsis*	*Trimeris* (in *Lobelia*)	*Commidendrum* (in *Felicia*) *Melanodendron* (in *Felicia*)		

* *Plocama* has been increased in size to include *Aitchisonia*, *Choulettia*, *Jaubertia*, *Pterogaillonia*, and *Putoria* (Backlund et al., 2007).

Table 4. Summary of taxonomic impact of new molecular (or other evolutionary) studies on the status of endemic genera in oceanic islands or archipelagos.

			Based on molecular phylogenetic studies, genus nested within a larger parental genus		
Island or archipelago	Genera still accepted	Genera submerged based on non-cladistic results	Genera still recognized	Genera submerged into parent (without combinations)	Genera submerged with combinations
Hawaiian Islands	22	1	8		3
Canary Islands	20	2		6	2
Robinson Crusoe Islands	7	2	1		2
St. Helena	7	1	2		
Galápagos Islands	4		3		
Bonin Islands	1	1			
Madeiran Islands	3		1		1
Totals	64	7	15	6	8

The situation with regard to recognition of genera in oceanic islands, however, is somewhat different from other types of examples. Endemic genera in oceanic islands must evolve from immigrants that come from some source area, usually a continental region. Immigrants that are particularly successful in dispersing to islands often come from large and diverse continental genera, which have been evolutionarily successful due to a high ability for dispersal, adaptation, and character divergence. Once in the islands, the lineage may adapt and diversify further, either anagenetically if the islands offer limited ecological opportunities (Stuessy et al., 2006), in which case endemic genera do not develop, or cladogenetically resulting in adaptive complexes of related species. If divergence continues rapidly, these complexes may be so divergent that they are now regarded as genera distinct from their continental progenitors. Because this process is relatively rapid, the degree of molecular divergence may be less than morphological divergence. This may be because genes regulating adaptive features diverge more quickly than neutral or near-neutral markers, which are those that are often used to measure genetic divergence.

If cladistic analysis, using any type of comparative data, reveals that an island genus is nested within a larger paraphyletic progenitor, then there are three taxonomic options: (1) the genus can be submerged in the larger continental genus, hence removing the paraphyletic status of the latter; (2) one might elect to split the larger genus into as many smaller genera as needed to allow all lineages to become holophyletic; or, (3) one can simply recognize a large paraphyletic parental genus and a divergent holophyletic island genus.

The data reveal that those working in molecular phylogeny have so far not automatically acted to submerge island endemic genera into their continental progenitors. In fact, of the 29 cases listed in Table 4, only in eight have the actual transfers and combinations been made. This suggests a hesitation

Table 5. Numbers of endemic genera of angiosperms now accepted in seven oceanic islands/archipelagos in comparison with numbers of genera if strict cladistic holophyly (to avoid paraphyly) were applied taxonomically in all groups, showing percent change.

Island or archipelago	Number of endemic genera now accepted	Number of endemic genera resulting under strict holophyly	% change (loss) in number of endemic genera
Bonin Islands	1	1	0.0
Canary Islands	28	20	28.6
Galápagos Islands	7	4	42.9
Hawaiian Islands	33	22	33.3
Madeiran Islands	5	3	40.0
Robinson Crusoe Islands	10	7	30.0
St. Helena	10	7	30.0
Totals	94	64	31.9*

* Does not include Bonin Islands.

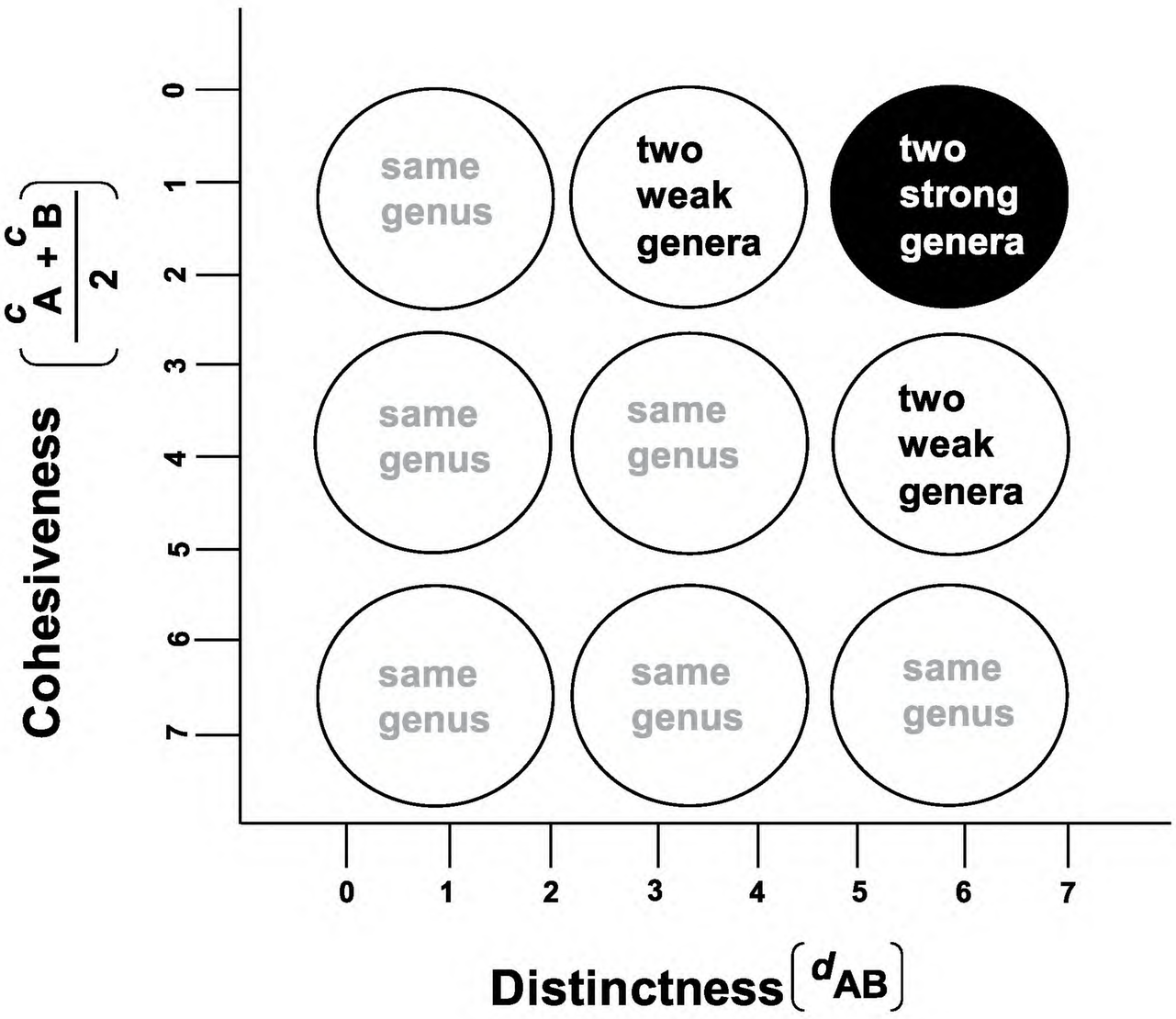


Figure 1. General relationship between cohesiveness and distinctness and the recognition of genera.

on the part of the participating investigators, perhaps for several reasons. First, it may be recognized that island taxa diverge rapidly due to strong directional selection and, using the generic level within the taxonomic hierarchy to emphasize this morphological divergence, may seem a logical alternative. Second, to some workers, simply because a group evolves from out of another group is no reason theoretically to have to submerge taxonomically the diverging unit back into the parental stock. Third, and perhaps most importantly, there may be hesitation to remove some of the endemic genera because in some cases they may be regarded as symbols of local (or national) pride or conservation importance in the island or archipelago. In the Robinson Crusoe Islands, for example, removal of the two largest endemic genera, *Dendroseris* (11 species) and *Robinsonia* (7 species), would reduce the conservation visibility to a considerable extent. As one specific example, the morphologically striking *D. litoralis*, nearly extinct in the wild, is grown in the village of San Juan Bautista as a source of island pride and identity. Conservation ethics do not (or should not) dictate scientific conclusions. But one has to wonder in this case if loss of endemic generic status of numerous morphologically divergent island taxa, simply to preserve the theoretical (cladistic) perspective of holophyly of continental progenitors, really makes any sense, scientific or otherwise.

These considerations bring us back to the question of how to recognize genera. A more sensible approach, in our view, is to evaluate generic status of a group not by simple reliance on holophyly, but by considering three dimensions taken together: (1) monophyly (in a broad sense), that is, not accepting polyphyly but admitting holophyly and paraphyly, (2) cohesiveness within the group, and (3) distinctness of the group from other known groups. Above all, the objective is maximum information content (high predictive quality) for our classifications, this being maximized by taking all evolutionary change into consideration, not which supports only the branching pattern.

Predictive quality (P) involving two genera, therefore, can be defined as:

$$P = ({}^{d}AB/{}^{c}A + {}^{c}B)/2$$

where d equals the distinctness between genera A and B, and c is the cohesiveness of genera A and B. Distinctness is measured by the character distance between the centers of the two groups (using a centroid method; Sneath & Sokal, 1973). Cohesiveness is the average character distance among group members (easily computed mathematically).

This statistic provides a yardstick for evaluation for generic recognition. Clear genera should give a predictive quality in the neighborhood of 5.0 or higher. Weak genera are at 1.0–2.0, and if P drops below 1.0, there is no argument for recognizing more than one genus. Figure 1 provides a visual scale that emphasizes that, as cohesiveness and distinctness increase, so does the argument for generic recognition.

Measuring predictive quality in this way is not phenetics. Phenetics is estimation of relationship by means of overall similarity, using as many characters as possible and without regard for evolutionary significance (Stuessy, 2009). In cladistics, one selects fewer characters of presumptive evolutionary import, uses them to assess relationships, and then uses only the synapomorphies to construct the branching diagram (cladogram). The main reason that cladistic classification is appealing is that it allows a classification to be converted conveniently (i.e., unambiguously) into a cladogram and the reverse. The cost of this, however, is to ignore part of the data (as uninformative) that we initially designated as evolutionarily significant. Phyletics (quantitative evolutionary classification) uses the same initial character information as cladistics, but all of it is assessed for purposes of developing predictive classifications because the autapomorphies that relate to divergence within lineages are also taken into account.

Quantitative morphological and/or genetic divergence is also not the entire picture for consideration with regard to generic recognition, especially that of endemic genera in islands. *Robinsonia*, for example, is nested within *Senecio* based on ITS sequence data (Pelser et al., 2007, 2010a), and new analyses by P. López (unpubl.) from data deposited in GenBank by Pelser et al., show a low *P* value of 1.43. This statistic of predictive quality shows that there is no greater molecular divergence of *Robinsonia* from species of *Senecio* than among other species within the genus. Based on these data and this statistic, there is no strong argument for keeping *Robinsonia* distinct from *Senecio*. Kim et al. (2007), in fact, made this same type of argument with respect to the large genus *Sonchus* and the incorporation of several generic segregates, including *Dendroseris* from the Robinson Crusoe Islands. These two endemic genera in the archipelago, however, are quite divergent morphologically despite low levels of measurable molecular divergence from progenitors using standard markers. *Robinsonia* contains species that are rosette trees and are dioecious, the morphological combination of which apparently does not occur within *Senecio* of continental South America. *Dendroseris* has species with different unusual morphologies, including being tall rosette trees, and one subgenus also being hummingbird pollinated, all very divergent morphologically from typical *Sonchus*. These morphological changes are, in fact, genetic and evolutionary responses of immigrant lineages into new oceanic island environments (Carlquist, 1974), and these can provide a basis for generic recognition.

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